

1160 W. Orange Grove Ave., Arcadia, California, U.S.A.
© Copyright 1971

NOTES ON
THE BIOLOGY OF *POANES VIATOR*
(HESPERIIDAE)

WITH THE DESCRIPTION OF A NEW SUBSPECIES

ARTHUR M. SHAPIRO¹

Department of Entomology and Limnology, Cornell University,
Ithaca, New York 14850

POANES VIATOR (EDWARDS), THE BROAD-WINGED SKIPPER, is the largest species of the subfamily Hesperinae in the north-eastern United States, but its life history and distribution have until recently remained no better known than they were when it was described in 1865. Laurent (1908) was unable to rear larvae from western New York ova. The first significant biological information was published by Kendall in 1966. Ten years ago I began observing a large population at Philadelphia, Pennsylvania, and since 1966 have been able to compare it in various respects to several smaller populations in central and western New York. Examination of long series and of the scanty literature, and correspondence with persons acquainted with the insect, confirm the field studies in suggesting that the Atlantic Coastal Plain populations of *P. viator* are subspecifically differentiated from those located near the Great Lakes.

It is unfortunate that Edwards's types apparently included both subspecies (Edwards, 1865). His description is based on one of each sex; a male "taken by Arthur Christie in northern Illinois," figured on his plate 1, fig. v, and a female collected by Norton at New Orleans, and not figured. The figured male is clearly of the Great Lakes subspecies. Holland (1931) figured as the "types" of *viator* two specimens from the Edwards collection in the Carnegie Museum, which have been identified by H. K. Clench as a male from Ontario and a female from Texas, and therefore "pseudotypes." The real types are at neither the Carnegie Museum nor the American Museum of Natural His-

¹ Present address: Division of Science and Engineering, Richmond College, 50 Bay Street, Staten Island, New York 10301.

tory, and must be assumed lost. The Coastal Plain subspecies of *P. viator* is better known than the Great Lakes one, but Edwards based his description almost entirely on the Illinois male; the Great Lakes subspecies should thus be taken as the nominate one. It seems desirable to fix this usage through a neotype designation. Strangely, until 1969 the only Illinois record of *P. viator* was Christie's original male; no specimens could be found in the American Museum, Carnegie Museum, United States National Museum, Cornell University, Museum of Comparative Zoology (Harvard), Field Museum of Natural History, or Illinois Natural History Survey collections. Through the kindness of Roderick R. Irwin of the I.N.H.S. an authentic pair of Illinois *P. viator* has been located, and I designate the male as neotype of *Poanes viator* Edwards and therefore of the nominate subspecies. This specimen has the postmedial spots of the hindwing beneath better developed than most *P. v. viator*, but the female taken with it is more "typical."

Neotype.—A male deposited in the Illinois Natural History Survey bearing the manuscript label "Goose Lake Prairie / Grundy Co. Ill. / 28-vii-69 / E. D. Cashatt" (fig 1, a, c). I have added a label identifying the specimen as the neotype of *P. viator*. Grundy County is in northwestern Illinois. A female with identical data (fig. 1, b, d) is also in the I.N.H.S. collection.

Poanes v. viator should be understood to apply to all the inland populations around the Great Lakes from central New York on the east to eastern North and South Dakota on the northwest and eastern Nebraska on the southwest (Shapiro, 1970). The Coastal Plain subspecies is here designated:

***Poanes viator zizaniae*, new subspecies**

(figure 2, a-j)

Holotype male (fig. 2, e) — Expanse, 33.0 mm. Length of left forewing, 19.9 mm. Upper surface dark brown marked with golden yellow as figured. Lower surface of forewings golden brown, suffused with blackish brown below vein M_3 , but paler at the outer margin; spots golden yellow, a blackish-brwn dot at end of cell. Lower surface of hindwings golden brown with a large dull yellow blotch consisting of four spots: a small one in the middle of cell RS; one in cell M_1 filling the middle third, just enclosing a dot of the ground color at its basal end; one nearly filling the basal half of cell M_3 ; and one in cell Cu_1 ,

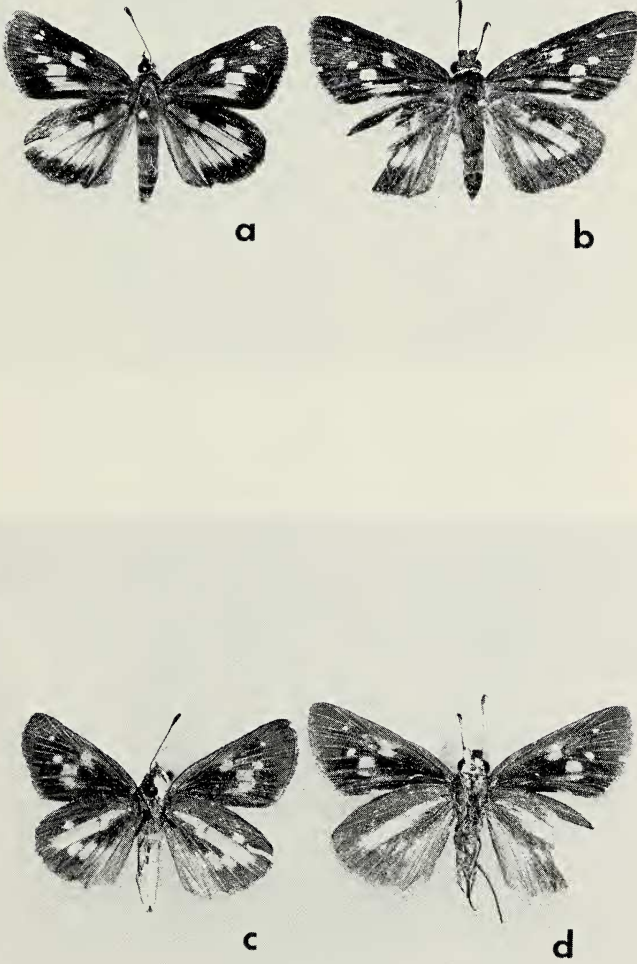


Fig. 1—a, c: *Poanes viator viator*, neotype ♂, Goose Lake Prairie, Grundy Co., Ill., vii.28.69. b, d: ♀, same data.

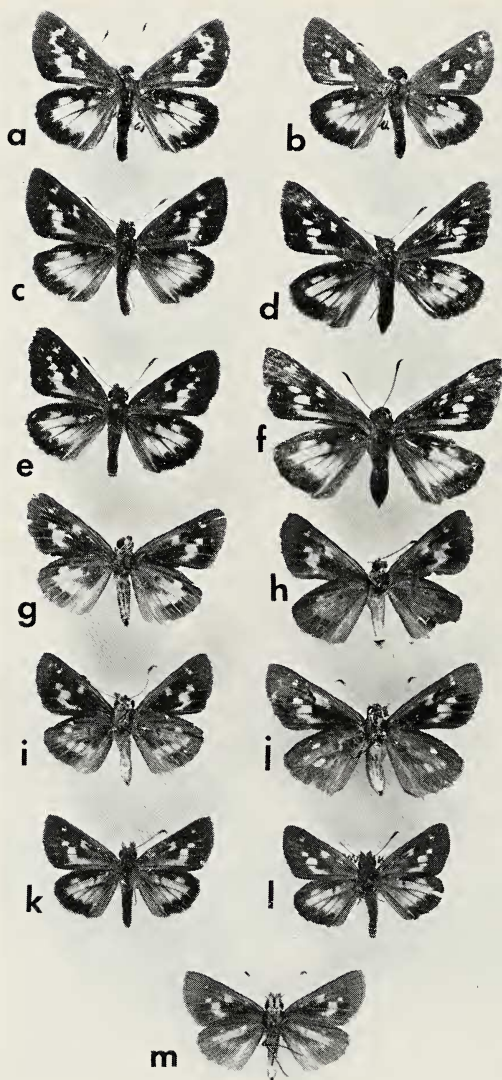


Fig. 2. a-j—*Poanes viator zizaniae* from Tinicum Wildlife Preserve, Philadelphia, Pa. a, paratype ♂, vii.20.65; b, paratype ♂, vii.20.65; c, paratype ♂, vii.16.66; d, allotype ♀, vii.16.65; e, holotype ♂, vii.16.65; f, paratype ♀, vii.20.65; g, "light" paratype ♂, vii.16.65; h, "dark" paratype ♂, vii.16.65; i, "intermediate" paratype ♂, vii.20.65; j, paratype ♀, vii.9.66. k-m: *Poanes v. viator*, Tamarack, Clinton Co., Pa. vii.19-20.65, 3 ♂.

extending from 1/5 the distance distad to the middle. Anal area paler than the ground color, with a pale shade extending to the base. Fringes, body and appendages as in the nominate subspecies.

Allotype female (fig. 2, d). — Expanse, 40.0 mm. Length of left forewing, 22.7 mm. Upper surface of forewings dark brown with lighter spots as in the nominate subspecies, as figured: those above Cu_1 white, that in cell Cu_1 white tinged with yellow, and the elongate spot in cell Cu_2 golden yellow, especially the part below the trace of A_1 . Upper surface of hindwings dark brown, the discal area golden yellow. Lower surface of forewings dull brown, vaguely greenish, suffused in the same pattern as the male, the spots golden yellow except the two subapical dots nearly white. Lower surface of hindwings golden brown, vaguely greenish, the pattern as in the male but olivaceous buff, not contrasting. Fringes, body and appendages as in the nominate subspecies.

Holotype male: Tinicum Wildlife Preserve, Philadelphia County, Pennsylvania, vii.16.65, leg. A. M. Shapiro. *Allotype female*: Same data. Both types deposited in Cornell University. *Paratypes*: 99 males and 27 females as follows: from the Tinicum Wildlife Preserve, Philadelphia: 25 ♂ 5 ♀, vii.22.67; 15 ♂ 2 ♀, vii.16.66; 16 ♂ 12 ♀, vii.20.65; 4 ♂ 3 ♀, vii.9.66; 27 ♂ 3 ♀, vii.16.65; 2 ♂ 2 ♀, vii.23.66; all leg. A. M. Shapiro. Also 10 ♂, Guadalupe County, Texas, iv.9.67, leg. R. O. Kendall. Paratypes will be distributed among the American Museum of Natural History, the Academy of Natural Sciences of Philadelphia, Cornell University, the Carnegie Museum, and the United States National Museum. Specimens of the new subspecies, mostly from New Jersey and the New York City area, are numerous in the collections of the major eastern museums. Additional toptotypical material is in the private collections of Mr. George Ehle of Lancaster, Pa. and Mr. Joseph Smaglinski, Reading, Pa.

Poanes viator zizaniae is named for its foodplant, being the genitive of *Zizania* L. The name applies to all populations from coastal New England to Texas, east of the Appalachian Mountains (figure 3).

The two subspecies differ in size and pattern, but no significant differences were found among the genitalia of males from Tinicum, Texas, and western New York.

The length of the left forewing (LFW) was compared for random samples collected in Pennsylvania colonies of both subspecies (Table 1):



Fig. 3.—Distribution of *Poanes viator*. Dotted line separates Coastal Plain *P. v. zizaniae* from inland *P. v. viator*.

Table 1

	<i>P. v. viator</i> ^a		<i>P. v. zizaniae</i> ^b	
	♂	♀	♂	♀
N =	24	12	25	6
LFW =	15.90 mm	19.70 mm	19.44 mm	21.70 mm.
s.d. =	0.46	0.61	0.58	1.08

^aTamarack, Clinton Co., Pa., vii.19-20, 1965

^bTinicum Wildlife Preserve, Philadelphia Co., Pa., vii.22-67.

Using a standard t-test (Snedecor, 1940), these means differ at the .01 level in each sex. This difference holds equally well for all populations for which a reasonable sample has been seen, and was first remarked for a series from Lanoraie, Quebec, described by Forbes (1960) as a "pauperized race." This series (in the Canadian National Collection) has been examined and is not significantly smaller than specimens from western and central New York.

The few Nebraska specimens seen, collected by Leussler, are larger than other *P. v. viator* but have the same pattern on the hindwing beneath. They differ from all other populations in consistently having yellow spots in cells M_1 and M_2 of the forewing above. This character occurs with relatively low frequency in populations of both subspecies; it is infrequent (less than 5%) at Tinicum. Texas specimens are slightly smaller than other *P. v. zizaniae* but have the underside pattern of that subspecies.

In *P. v. zizaniae* the blotch in the middle of the hindwing beneath is relatively broad; the postmedial spots are well developed, longer (basal-distal) than wide; the elongate yellow spot in M_1 is cut off squarely just basad of the included dark submedial dot, and never reaches the base. In *P. v. viator* the postmedial spots are small, indistinct, and usually rounded; the spot in M_1 is longer and more contrasting, reaching as a pale shade to the base (fig. 2, m). A few specimens lack the postmedial spots but have the spot in M_1 a yellow streak from the base nearly to the margin. The usual pattern produces an effect similar to that of the same wing in *Euphyes dion* Edwards and *Poanes howardi* Skinner. *P. v. viator* often occurs with *E. dion* and may be difficult to tell from it in the field.

Forbes (1960) notes that the hindwing blotch beneath may be either "weak" or "contrasting". Male *P. v. zizaniae* divide easily into three grades based on this character (fig. 2, g-i). The female pattern (fig. 2, j) is more obscure, and mono-



Fig. 4.—The habitat of *Poanes viator zizaniae* in the Tinicum Wildlife Preserve, Philadelphia, Pa., vii.27.66. *Zizania* forming solid stand in background.

morphic. Every Coastal Plain series examined, including Texas, is trimorphic in the male. A random sample of 94 *Tinicum* males taken in 1966 included 25 "dark" (0.27), 41 "intermediate" (0.44), and 28 "light" (0.30). If the three grades represented the genotypes produced by a single allele pair with frequencies of 0.5, these figures would very closely approximate the Hardy-Weinberg equilibrium values. The genetics of the polymorphism is, of course, totally unknown. The three grades, "dark," "intermediate," and "light," roughly correspond phenotypically to *Poanes massasoit* Scudder forms *suffusa* Laurent, *hughi* Clark, and typical, respectively. Similar phenotypes occur in *P. yehl* Skinner (Mather and Mather, 1958) and *P. hobomok* Harris. In *P. massasoit* and *P. hobomok* the three grades often do not occur together in the same populations, suggesting they are not allelic. The genus *Poanes* is often considered polyphyletic (cf. Klots, 1951). The holotype of *P. v. zizaniae* belongs to the "intermediate" grade.

A few male *P. v. zizaniae* have the blotch beneath very clear yellow and of the same shape as in *P. hobomok*. Such males also have the light markings enlarged above, frequently including the light spots in cells M_1 and M_2 of the forewing (fig. 2, a).

The phenotype of *P. v. viator* is essentially monomorphic. Nothing like the "dark" form has been seen in this subspecies. Rarely the long spot in cell M_1 is tinted slightly reddish.

BIOLOGY

Food Plant. — At Tinicum and Bombay Hook, Delaware, *P. v. zizaniae* feeds on wild rice, *Zizania aquatica* L. (Gramineae). In Texas, Kendall (1966) found it on the closely related grass marsh millet, *Zizaniopsis miliacea* (Michx.) Doell. & Arch. The geographic range of *Z. aquatica* alone (Hitchcock, 1935) includes the entire range of *P. v. viator*, but it may have been introduced to much of this area by the Indians. *Zizania* has a disjunct eastern North American-eastern Asia (Arcto-Tertiary relict) distribution (Fernald, 1950), probably having survived the Pleistocene in the southeast. There is no evidence that *P. v. viator* ever feeds on *Zizania*, and it is often found in places where this plant does not grow. Miller (1961) found it associated with an undetermined bog sedge in north-central Iowa. In New York and Pennsylvania it and *Euphyes dion* are both associated with and oviposit on *Carex lacustris* Willd. (*Carex riparia*, var. *lacustris*, of authors). This was reported by Heitzman (1964) as a food of *E. dion* in the Midwest. It is also a

food plant of *Lethe appalachia* Chermock (Satyridae) (Shapiro and Cardé, 1970). Both Fernald (1950) and Wiegand and Eames (1926) record this sedge from shallow water in circum-neutral to alkaline marshes, but it also occurs in acid waters; its role in Minnesota bogs is described by Conway (1949). Its range is given by Fernald as "Anticosti I., Quebec to S. Manitoba, south to Nova Scotia, New England, Virginia, Ohio, Indiana, Illinois, Iowa, and South Dakota." This resembles the range of *P. v. viator*, excluding only Nebraska.

Pre-oviposition behavior by female *P. v. zizaniae* directed toward reed, *Phragmites communis* L., has been observed twice at Tinicum, but no eggs could be found. *Phragmites* is suspected as a food plant of this subspecies in Connecticut (C. L. Remington and R. T. Cardé, pers. comm.). It is acceptable to large larvae taken from *Zizania*, but newly hatched larvae have not been tested. *Phragmites* is believed to be non-native to North America.

Large larvae of *P. v. zizaniae* are easily found on the food plant at Tinicum. The larva of *P. v. viator* has not been collected in the wild.

Habitat. — *Poanes viator zizaniae* usually occurs in fresh to brackish marshes in which the food plant, *Zizania*, forms extensive stands in shallow water; such habitats have been described in Virginia (Clark and Clark, 1951) and Georgia (L. Harris Jr., pers. comm.) as well as in Pennsylvania and New Jersey (Shapiro, 1966). The vegetation of the Tinicum marsh is described by McCormick (1970); this is the largest remnant (about 400 acres) of the tidal marshes of the Delaware, which once extended from the lower bay to Bristol, Pa. and whose vegetation was described by Smith (1867) and Harshberger (1904). *P. v. zizaniae* occurs mostly in the true marsh near *Zizania*, (fig. 4), but visits flowers freely—often well away from the food plant, particularly in the males. Species often visited are pickerelweed, *Pontederia cordata* L.; purple loosestrife, *Lythrum salicaria* L.; blue vervain, *Verbena hastata* L.; and buttonbush, *Cephalanthus occidentalis* L. Species common in *P. v. zizaniae* habitats, but not visited, are swamp rose-mallow, *Hibiscus moscheutos* L., and primrose-willow, *Jussiaea repens*.

The habitats of *P. v. viator* are frequently much less open and extensive. Miller found it in an overgrown, sedgy peat bog in Iowa. Sheppard (pers. comm.) found it at Lanoraie, Quebec in

a "willow swamp with sedges" and Holmes (pers. comm.) in a "small marsh . . . among the rushes" at Brantford, Ontario. Its New York and Pennsylvania habitats are mosaics of relatively open sedge marsh and dense bush swamp. Some characteristic plant associates are poison sumac, *Rhus vernix* L.; winterberry, *Ilex verticillata* (L.) Gray; alder, *Alnus* spp.; swamp milkweed, *Asclepias incarnata* L., and Joe-Pye weed, *Eupatorium* spp. The now-extinct Ithaca colony, destroyed by flood control dredging and filling in 1968, was located in a two-acre *Carex lacustris*-*Typha* marsh heavily overgrown with willow and tall herbs on the drier sites. It was a relict of the once extensive sedge-cattail marshes at the mouth of Cayuga Inlet. *P. v. viator* still occurs in the relatively undisturbed marshes at Monetzuma, New York, at the north end of Cayuga Lake.

Flight Period — *P. v. zizaniae* at Tincicum flies just before the middle of July through early August, peaking about July 20. This single, short flight corresponds to other northern Coastal Plain records (Comstock, 1940; Davis 1910; Beutenmuller 1893, 1902; Forbes, 1928). The Clarks (1951) give a confusing picture for Virginia. At most localities they find no evidence of more than one flight, but the dates for the entire state divide into two groups: June 6-July 5 and July 25-September 2. In Richmond County the species was found on June 27, 1937 and August 31, 1941 at the same locality. Probably *P. v. zizaniae* is bivoltine in coastal Virginia and the uncertainties reflect only inadequate collecting. This is certainly true in Georgia, where Harris (pers. comm.) records it from late April-late May and late September-early November, again not in the same localities. There should be a midsummer brood as well. Florida records (Kimball, 1965) are fragmentary: April and August. Kendall (1966) records four broods in eastern Texas.

P. v. viator is single-brooded everywhere, including Nebraska (Leussler, 1939). The flight is mainly in July. In Central New York it begins a bit earlier than Coastal Plain *P. v. zizaniae* farther south (as early as July 3 at Ithaca) and extends into early August (August 3, Texas Hollow, Schuyler County).

Population Structure. — The Tincicum colony of *P. v. zizaniae* was studied by the Lincoln index mark-recapture method (cf. Ford, 1957) to obtain an estimate of population size in 1965 and 1967. The insects are easily captured and generally well suited to capture-recapture study. The resulting values were 12,000-15,000 in 1965 and 4,000-6,000 in 1967. Most populations

of *P. v. viator* are much sparser than this; of the upstate New York colonies, only Montezuma and the Oak Orchard Swamp have large enough populations to make similar studies feasible. The sparseness of these populations may be due to the nature of the habitat, but interspecific aggression by territorial male *Euphyes dion* against the non-territorial *P. v. viator* males and females was frequently observed, and may be a significant factor in limiting their population density. Since both species feed on the same sedges, it may also be relevant to competition for oviposition sites or larval food, but almost nothing is known of the nature or even the reality of such competition in butterflies (Clench, 1967).

Adult Behavior. — Both subspecies of *Poanes viator* are non-territorial. In this they resemble other marsh and bog butterflies such as *P. massasoit* and *Lycaena epixanthe* Boisduval and Le Conte. Such species occur in a sharply defined habitat, often at high densities, while their more wide-ranging, ecologically tolerant relatives (e.g. *Poanes hobomok* and *Lycaena phlaeas* Linnaeus) are less concentrated spatially and show male territoriality. *Euphyes dion* and *E. bimacula* Grote and Robinson are marsh butterflies which are territorial and normally maintain sparse populations despite the circumscribed nature of their habitat. During a population outbreak of *E. bimacula* in central New York in 1968, this behavior was suppressed (Shapiro, unpublished). *E. dion* rarely exceeds a population density of two pairs per acre in upstate New York.

Both subspecies of *P. viator* seem to display intrinsic barriers to dispersal (Ehrlich, 1961). Although males and, less frequently, females may leave the vicinity of the larval food plant to feed, neither sex has been observed out of (human) sight of the areas of highest population density. Actually dispersal data are unavailable because of the large distances separating the colonies observed. Estimates of movement among patches of suitable habitat within large mosaic areas such as the Montezuma marsh and the Oak Orchard Swamp may be obtainable. At Ithaca, *P. v. viator* failed to colonize seemingly suitable habitats within one-half mile of the now extinct Cayuga Inlet colony.

Both sexes usually fly below the top of vegetation, twisting among wild rice or sedge blades from one to three feet above the ground or water surface. Eggs are laid singly on the underside of a blade of the food plant, usually near the middle or below it; the female clings to the edge of the blade and curves

the abdomen underneath it to lay.

Larval Behavior. — Kendall (1966) reports that Texas larvae of *P. v. zizaniae* construct no formal shelter, living instead in the recess at the base of the leaf on which they feed. Tinicum larvae do reinforce this area with silk before molting. At least after the last molt, the larva frequently moves to a new leaf. It always feeds above the water line. Large larvae collected in late August pupate within two or three weeks and produce adults from ten to thirty days later. This is similar to Kendall's experience in Texas, where a larva collected 19 June pupated 24 June and eclosed 2 July. Obviously, this is not the normal developmental rate at Tinicum.

Zizania is an annual which dies before hard frost, and later falls over in the water. By September 15 no trace of larvae can be found on the plants, nor have larvae or pupae been found in the *Zizania* remains in midwinter. Apparently the larvae leave the stand when mature; if they overwinter on land they must be capable of swimming or rafting a distance of at least a few hundred yards. Kendall found summer pupae in the larval nests, but does not know how the species overwinters in Texas.

SUMMARY

1. *Poanes viator* Edwards is divided into two subspecies, *P. v. viator* and *P. v. zizaniae*, new subspecies.
2. *P. v. viator* is restricted to the sedge-feeding populations distributed around the Great Lakes from central New York to Nebraska, characterized by smaller size, monomorphic ventral hind wing pattern, and univoltinism.
3. *P. v. zizaniae* (type locality Tinicum Wildlife Preserve, Philadelphia, Pa.) is distributed on the Atlantic Coastal Plain from New England to Texas. It feeds on *Zizania* (and possibly *Phragmites*), is larger than *P. v. viator*, has a trimorphic ventral hind wing pattern in males, and is multi-voltine from Virginia south.

ACKNOWLEDGMENTS

Many individuals and institutions contributed to this investigation by providing records or making specimens available for study. I wish to thank: the late R. G. Beard; F. M. Brown; R. T. Cardé; H. K. Clench (Carnegie Museum); C. V. Covell,

Jr.; M. G. Emsley (Academy of Natural Sciences of Philadelphia); W. D. Field (U.S. National Museum); T. N. Freeman (Canadian National Collection); J. M. Fogg, Jr. (University of Pennsylvania Herbarium); D. F. Hardwick (Canadian National Collection); L. Harris, Jr.; R. Heitzman; A. M. Holmes; R. Irwin (Illinois Natural History Survey); R. O. Kendall; C. P. Kimball; A. B. Klots (American Museum of Natural History); B. Mather; L. D. Miller; Col. S. S. Nicolay; L. L. Pechuman (Cornell University); N. D. Riley (British Museum — Natural History); J. C. E. Riotte (Royal Ontario Museum); A. C. Sheppard; M. E. Smith (University of Massachusetts); J. Wilcox (New York State Museum).

LITERATURE CITED

- BEUTENMULLER, W. 1893. Descriptive catalogue of the butterflies found within fifty miles of New York City. *Bull. Amer. Mus. Nat. Hist.* 5: 241-310.
- , 1902. The butterflies of the vicinity of New York City. Guide leaflet 7, suppl. to Amer. Mus. Journal, v. 2.
- CLARK, A. H. and L. F. CLARK. 1951. Butterflies of Virginia. *Smithson. Misc. Coll.* 116(7): 239 pp.
- CLENCH, H. K. 1967. Temporal dissociation and population regulation in certain Hesperine butterflies. *Ecology* 48: 1000-1006.
- COMSTOCK, W. P. 1940. Butterflies of New Jersey. *J. New York Ent. Soc.* 48: 47-84.
- CONWAY, V. M. 1949. The bogs of central Minnesota. *Ecol. Monog.* 19: 175-225.
- DAVIS, W. T. 1910. List of the Macrolepidoptera of Staten Island, New York. *Proc. Stat. I. Assn. Arts Sci.* 3: 1-30.
- EDWARDS, W. H. 1865. Description of certain species of diurnal Lepidoptera found within the limits of the United States and British America. IV. *Proc. Ent. Soc. Phila.* 4: 201-204.
- EHRlich, P. R. 1961. Intrinsic barriers to dispersal in checkerspot butterfly. *Science* 134: 108-109.
- FERNALD, M. L. 1950. Gray's Manual of Botany. Eighth edition. New York: American Book Co. 1632 pp.
- FORBES, W. T. M. 1928. Lepidoptera. in W. D. Leonard, ed. A list of the insects of New York. *Cornell Univ. Agr. Expt. Sta., Mem.* 101. pp. 532-687.
- , 1960. The Lepidoptera of New York and neighboring states. IV. *N. Y. State Agr. Expt. Sta. Mem.* 371: 188 pp.
- FORD, E. B. 1957. Butterflies. Third edition. London: Collins. 368 pp.
- HARSHBERGER, J. W. 1904. A phyto-geographic sketch of extreme southeastern Pennsylvania *Bull. Torrey Bot. Club* 31: 125-159.
- HEITZMAN, R. 1964. Season summary. *Lepid. Soc. News*, 15 April.
- HITCHCOCK, A. S. 1935. Manual of grasses of the United States. *U.S. Dept. Agr. Mic. Publ.* 200: 1040 pp.
- HOLLAND, W. J. 1931. The Butterfly Book. Revised edition. Garden City, N. Y.: Doubleday Doran. 423 pp., 77 pls.

- KENDALL, R. O. 1966. Larval foodplants and distribution notes for three Texas Hesperidae. *J. Lepid. Soc.* 20: 229-232.
- KIMBALL, C. P. 1965. The Lepidoptera of Florida. Gainesville: State Dept. Agr. 363 pp.
- KLOTS, A. B. 1951. A field guide to the butterflies. Boston: Houghton Mifflin Co. 349 pp.
- LAURENT, P. 1908. Notes on the early stages of some *Pamphila*. *Ent. News* 19: 408-417.
- LEUSSLER, R. A. 1939. An annotated list of the butterflies of Nebraska, with the description of new species. (Lepid., Rhopalocera). *Ent. News* 50: 34-39.
- MATHER, B. and K. MATHER. 1958. The butterflies of Mississippi. *Tulane Stud. Zool.* 6: 64-109.
- McCORMICK, J. 1970. The natural features of the Tinicum Marsh, Delaware and Philadelphia Counties, Pennsylvania, with particular emphasis on the vegetation. The Conservation Foundation.
- MILLER, L. D. 1961. On nine Iowa butterflies, four new to the state. *J. Lepid. Soc.* 15: 97-98.
- SHAPIRO, A. M. 1966. Butterflies of the Delaware Valley. Phila.: *Amer. Ent. Soc.* 79 pp.
- , 1970. Postglacial biogeography and the distribution of *Poanes viator* (Hesperidae) and other marsh butterflies. *J. Res. Lepid.*
- SHAPIRO, A. M. and R. T. CARDÉ. 1970. Habitat selection and competition among sibling species of Satyrid butterflies. *Evolution* 24: 48-54.
- SMITH, A. H. 1867. On colonies of plants observed near Philadelphia. *Proc. Acad. Nat. Sci. Phila.* 19: 15-24.
- SNEDECOR, G. W. 1940. Statistical Methods. Third edition. Ames, Iowa. State College Press. 422 pp.
- WIEGAND, K. M. and A. J. EAMES. 1926. The flora of the Cayuga Lake basin, New York. *Cornell Agr. Expt. Sta. Mem.* 92: 491 pp.